

FLORAL BIOLOGY OF CALIFORNIA BUCKEYE

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California buckeye, *Aesculus californica* (Spach) Nutt., is a familiar tree or shrub of the Coast Ranges and Sierra Nevada foothills. Its phenology is unique among native deciduous trees, for although it is the first to leaf out in late winter, its leaves are the first to become senescent and die during midsummer. In contrast to this short active foliar period, the periods of floral and fruit development are quite long. Young inflorescences covered with hundreds of floral buds are exposed when leafing-out occurs; anthesis begins in spring and continues through early summer. Fruit development ensues from summer until winter when the large seeds are shed.

A closer look at California buckeye's reproductive method reveals anomalous features that apparently impede efficient sexual reproduction. For example, each spring trees are covered with candle-like inflorescences each bearing a profusion of odoriferous flowers that attract many insects; but apparently nectar and pollen are poisonous to honeybees, floral abscission is common, and relatively few capsules mature the following winter. The purpose of this study, therefore, was to examine the floral biology of California buckeye and in doing so to endeavor to resolve some of the presumptive paradoxes.

Study populations, each consisting of a stand of 40 or more buckeye plants within an area of about four hectares, were located throughout the species' range (fig. 1). Within each stand 20 individuals were tagged and used for analysis of floral form and occurrence, frequency, and distribution of bisexual flowers. Local populations in Alameda and Contra Costa counties (not shown in Figure 1) were used for experiments of floral development, pollination, and breeding behavior.

FLORAL FORM AND DEVELOPMENT

Inflorescence primordia are laid down in fall within buds that also contain leaf primordia. When buds break in February and March, the inflorescences exposed are 5 to 10 mm long and tightly surmounted with small, undeveloped floral buds. The inflorescence elongates during spring by means of intercalary growth producing a columnar panicle (thyrses). Each lateral branch (cincinnus) bears from five to seven floral buds that mature one at a time. Within a given cincinnus, the bud nearest the rachis is the first to mature; its pedicel elongates, thrusting it out over the other buds. Subsequent bud development proceeds outward, although in most cases the outermost three buds never complete enlargement and fail to open. Bud mortality is even higher under adverse climatic condi-

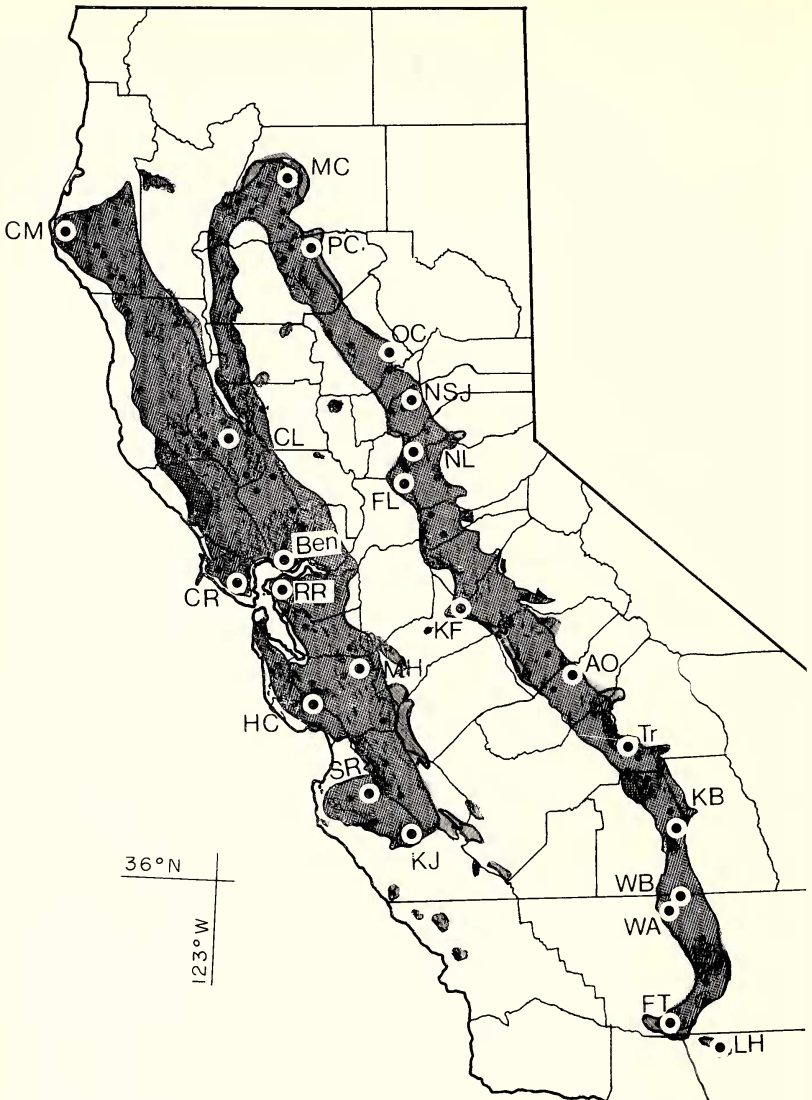


FIG. 1 Locations of study populations and the natural range of California buckeye.

tions, such as late frosts or early hot spells. Even with inherent bud mortality, an inflorescence may still bear over two hundred flowers.

Flowers of California buckeye are either bisexual or functionally staminate (fig. 2). In the former case, the gynoecium is fully developed and is composed of three fused carpels with two ovules per locule. In the staminate flower, the gynoecium is vestigial, with a stipitate, undevel-

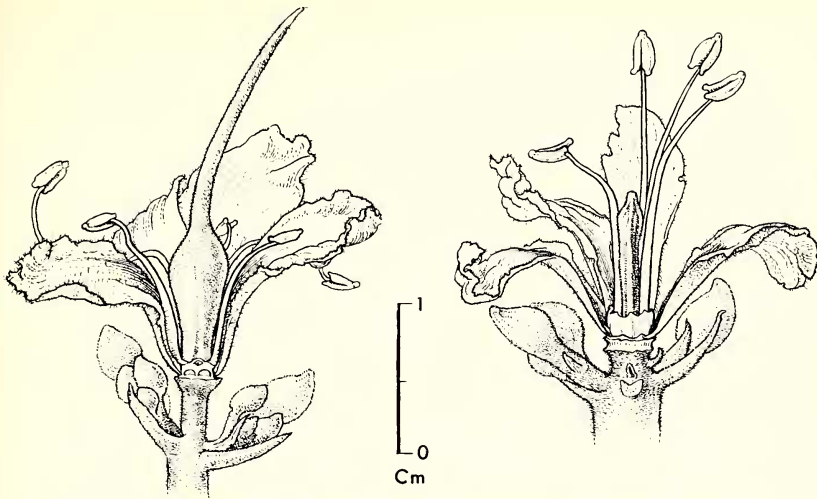


FIG. 2. Flowers of California buckeye. Left: bisexual; right: staminate.

oped ovary surmounted by a short, stubby style. Androecia of both kinds of flowers bear five to seven stamens, most of which are long-exserted at maturity.

After opening, a flower passes through a series of stages lasting 5 to 8 days. Bisexual flowers are protogynous. The flower commences anthesis with the emergence of the stigma and corolla through the enveloping calyx. The expanding white petals then reflex, exposing the villous pistil and orange anthers borne on short filaments. Yellow nectar guides then appear above the claws of the petals while the pistil with its long, pointed style completes its growth and the filaments begin to elongate. With maturation, nectar guides turn pink to red, filaments elongate, and anthers dehisce; short stamens may dehisce before the exserted stamens. Ovary enlargement continues after the perianth and stamens have fallen away. Many of the ovaries are abortive and fail to form fruits with viable seed.

Early development of the perianth and androecium in the staminate flower is similar to that of the bisexual flower. Filament elongation is rapid and stamens are longer than those of bisexual flowers. Staminate flowers fall from inflorescences more easily than bisexual flowers; nevertheless, premature abscission of young flowers of both types is common. Often they wither and drop off before the anthers have dehisced.

OCURRENCE, FREQUENCY, AND DISTRIBUTION OF BISEXUAL FLOWERS

Usually, the first flowers to open, the terminal flower and those that follow suit shortly afterwards, are staminate. There are trees, however, that produce inflorescences with terminal bisexual flowers or bisexual flowers early in the sequence of inflorescence development. Such behavior

is characteristic of inflorescences and trees that produce relatively high numbers of bisexual flowers throughout the flowering period. This early indication of high bisexual flower potential in some trees was observed at the Humboldt County population (CM).

In order to assess intra-panicle production of bisexual flowers, inflorescences from 12 study populations and miscellaneous collections from randomly selected trees were examined and the distribution and frequency of bisexual flowers within the inflorescences recorded. At each study area, a single inflorescence bearing bisexual flowers was picked at random from each tagged tree. Sampling was done only after trees were in full bloom. The effect of crown position and cardinal aspect was checked with no correlation or pattern of variation being readily apparent.

The majority of bisexual flowers were formed only in the upper portions of the inflorescences. Of 298 inflorescences examined, 55 percent had bisexual flowers restricted to the upper one-third of the inflorescence; in 23.5 percent, they were limited to the upper two-thirds while 21.5 percent had bisexual flowers distributed throughout the entire length of the inflorescence. None of the inflorescences examined had bisexual flowers restricted solely to basal cincinni. These data agree with Jepson's (1936) contention that bisexual flowers are generally formed near the terminal end of the inflorescence. Hardin (1956), on the other hand, stated that in *A. californica*, bisexual flowers were very often scattered throughout the inflorescence or occasionally occurred only near the top. In other species of *Aesculus*, bisexual flowers are restricted to the basal portion or more often occur in any part of the thyrses (Hardin, 1956).

Those populations that lacked inflorescences with bisexual flowers distributed throughout the entire length (MC, OC, KF) were notable in producing fewer inflorescences with bisexual flowers. Inflorescences with bisexual flowers distributed throughout the rachises occurred most frequently in the CM and KJ populations. Inflorescences from these stands also had the highest numbers of bisexual flowers (Table 1). Based on an average production of 200 flowers per inflorescence, the relative proportions of bisexual flowers approached, and in some cases exceeded, 25 percent. Three trees were noted to produce inflorescences in which up to 35 percent of the flowers were bisexual. In one tree at the KJ population, bisexual flowers failed to produce functional anthers, hence were pistillate. Failure of anther and pollen development was observed in occasional bisexual flowers from other individuals, but not to the extent achieved by this tree. Although the CM and KJ stands, respectively, occur near the northern and southern limits of the species' distribution in the Coast Range, they differ ecologically despite their similarities in floral behavior. The CM population, on Cape Mendocino, is on a windy, exposed, seaward slope, whereas the KJ population, near King City, is on a sheltered, sandy bench bordering oak woodland and dense chaparral.

TABLE 1. FREQUENCY OF BISEXUAL FLOWERS WITHIN INFLORESCENCES OF CALIFORNIA BUCKEYE. See Figure 1 for locations of study populations. N = 20.

Population sampled	Numbers of inflorescences per frequency class			
	0-4	5-10	11-20	more than 20
MC	5	10	5	0
OC	9	10	1	0
NSJ	4	8	8	0
KF	11	9	0	0
KB	5	11	4	0
WA	7	9	3	1
FT	3	14	2	1
CM	0	7	7	6
CR	2	12	4	2
RR	3	15	2	0
Ben	5	10	3	2
KJ	4	6	6	4
Totals	58	121	45	16
Misc. indiv.	13	22	15	8
Totals	71	143	60	24

With the exception of these two populations (CM, KJ), the overall frequency tally evinced the general observation that the production of bisexual flowers within inflorescences is low (Table 1). Even though about one-fourth (28.2 percent) of the inflorescences bore more than ten bisexual flowers per inflorescence, the ratio of bisexual to staminate flowers generally did not exceed five percent.

Modification of sex expression. It is not unusual to find on a given tree several inflorescences that are broken or mutilated to varying degrees. Inflorescences are often attacked by insects; moreover, inflorescences on lower branches and on low, shrubby California buckeyes are especially subject to browsing by deer. Closer examination of these inflorescences often reveals a high proportion of bisexual flowers among those remaining. While still in the bud stage, these inflorescences are often chewed and/or nipped in half, and many of the flowers that would have been staminate turn out to be bisexual. Of 227 naturally mutilated inflorescences scored in the field, 84 percent had bisexual flowers compared with 47 percent for nearby unmutilated inflorescences.

In order to ascertain whether this behavior could be induced, inflorescences at various stages of bud development were cut transversely in half. Trees at local populations with lower branches near the ground were selected for treatment; 175 inflorescences were mutilated and 175 control inflorescences were tagged. Following anthesis, the mutilated and control inflorescences were scored for the occurrence, frequency, and distribution of bisexual flowers. There was no correlation between time of mutilation, i.e., stage of inflorescence development, and subsequent formation and number of bisexual flowers. Overall, 63 percent of the muti-

lated and 54 percent of the control inflorescences bore bisexual flowers. Within trees, the total and mean numbers of bisexual flowers formed in the control and mutilated inflorescences did not differ significantly. When, however, only the lower portions of the inflorescences were compared, the differences were highly significant. The mutilated inflorescences bore 1,113 bisexual flowers as compared with 301 formed in the basal half of the control inflorescences. Mutilations failed to increase the total number of bisexual flowers, but did stimulate gynoecial development in the lower cincinni, the region in which few bisexual flowers are normally formed.

Variation of sex expression. In *Aesculus*, each individual plant supposedly produces both staminate and bisexual flowers, i.e., is andromonoecious. The degree of consistency of this condition within and between populations is unknown. Do some plants produce only one floral type, giving rise to some degree of androdioecism, or do they all produce both types? What proportion of inflorescences in a given tree actually form both staminate and bisexual flowers and how does this vary within and between populations?

Presence or absence of bisexual flowers was scored for the tagged trees plus 257 additional individuals at the study areas. Also, 792 individual buckeyes distributed throughout the species' range were examined and tallied as to whether or not they bore bisexual flowers. The procedure was to scan the crown with binoculars and tally with a counter. All inflorescences were scored in trees with less than 500 inflorescences. In trees with more than 500, the sample was in excess of 500 inflorescences and not less than approximately 25 percent of the total number of inflorescences on the tree.

Populations examined varied little from the andromonoecious condition, for all individuals produced staminate and most produced at least some bisexual flowers. Individual trees, however, differ in the proportions of inflorescences that bear bisexual flowers. Only seven (0.28 percent) purely staminate trees were found, while there were only four (0.16 percent) in which every inflorescence appeared to contain bisexual flowers. It is not uncommon to find individuals in which fewer than 10 percent or more than 70 percent of the inflorescences had bisexual flowers (fig. 3). In those with high proportions of inflorescences with bisexual flowers, the ratio of bisexual to staminate flowers also was high.

The basis for this overall bimodality becomes apparent when individual populations are analyzed. Histograms for each study population plotted by 25-percentile classes are shown in Figure 4. Most of the trees in the coastal populations produced bisexual flowers in over 75 percent of their inflorescences. Moving inland, no consistent pattern was discernible. Trees in four populations (NSJ, NL, FL, TR) produced relatively high proportions of inflorescences bearing bisexual flowers, while the southern stands level off to a certain extent, having more or less

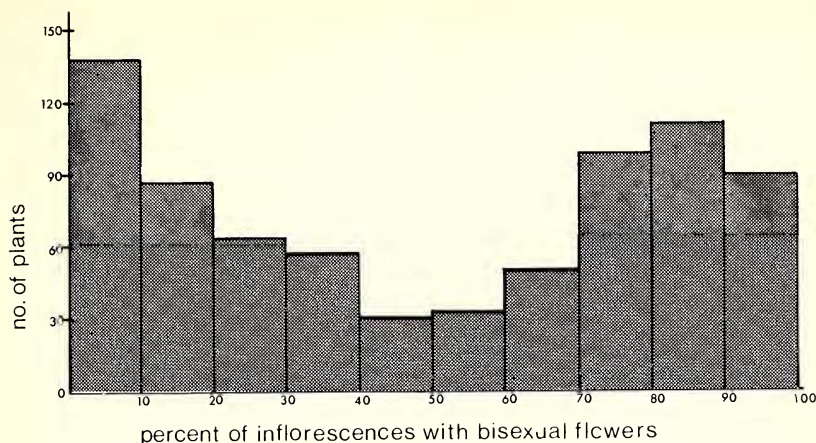


FIG. 3. Overall production of inflorescences with bisexual flowers in California buckeye.

equal numbers of trees in each class. Trees in the northeastern populations (MC, PC, OC), on the other hand, were notable in producing low proportions of inflorescences with bisexual flowers as were stands on the east side of the Mount Hamilton Range (MH) and in the Sierra Nevada foothills (KF). The low rainfall and extreme temperatures that characterize these inland habitats could be factors influencing sex expression. Climatic data from each site, however, would be necessary before attempting any specific correlations. Age of the plants might also be an important factor; in a sprouter like California buckeye, age of plant and age of aerial shoot are separate phenomena. The relative ages and form of the existing shoots that were included in the sample did not seem to influence production of bisexual flowers. Nevertheless, young sprouts were observed to form few, if any, inflorescences with bisexual flowers.

The relevancy of the above data depends on how they might vary with time. A 2-year survey in eight of the study populations showed an annual shift of 10 percent or less. Tally of 15 trees over an 8-year period indicated little year to year variation. Trees in extreme classes were most consistent.

POLLINATION AND BREEDING BEHAVIOR

Pollen grains of *Aesculus* are small and morphologically similar (Hardin, 1957); however, comparison with the published dimensions of other species indicate that the grains of *A. californica* are among the smallest, i.e., ca $19 \times 25 \mu\text{m}$. This is especially small for an entomophilous taxon. In addition, pollen production per anther is high, as is production on a flower, inflorescence, plant, or population basis.

Estimates of pollen production were based on counts of flowers and stamens from ten inflorescences randomly selected from collections from

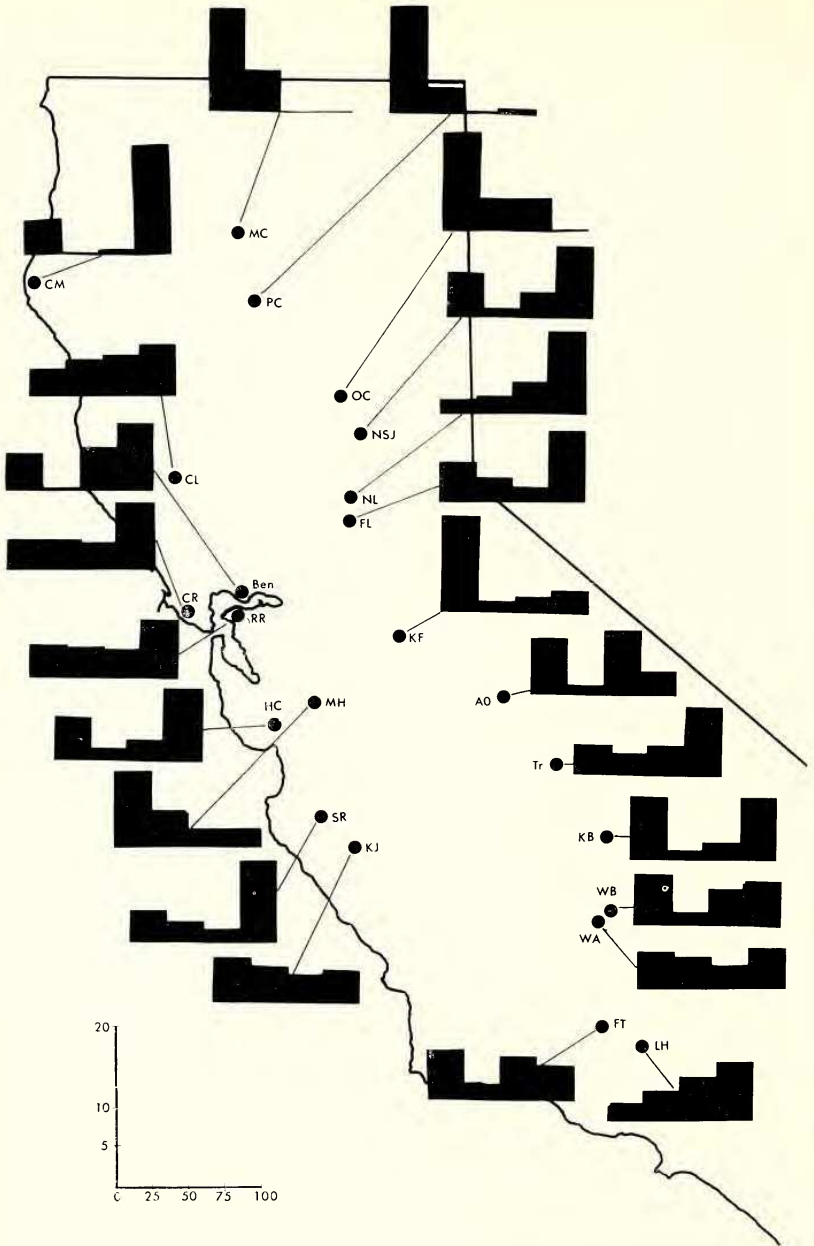


FIG. 4. Geographic variation in the production of inflorescences with bisexual flowers in California buckeye. Each histogram depicts relative proportions of inflorescences with bisexual flowers at each study population by 25-percentile classes. The vertical axis indicates numbers of plants.

the study populations. One anther per inflorescence was sampled. The number of pollen grains was estimated by emptying the contents of an undehisced anther into a drop of lactophenol-cotton blue on a slide. The pollen was evenly distributed with a needle and carefully covered with a coverslip. A 20 percent sample of the area under the coverslip was counted using a magnification of 100 \times and taking evenly distributed fields of view. The total number of grains estimated per anther ranged from 8 to 11 thousand. The stainability of the pollen generally exceeded 85 percent, so fertility presumably was quite high.

Pohl (1937) estimated that 42 million pollen grains are produced per inflorescence in *A. hippocastanum*; my estimate for *A. californica* is 19 million. He also gave a production figure of 451,543 pollen grains per ovule for *A. hippocastanum*; a conservative estimate for *A. californica* is 750,000. More meaningful as far as reproductive capacity is concerned is the number of pollen grains produced per seed. Most mature capsules in *A. californica* contain only one or two seeds even though the ovary of a bisexual flower forms six ovules (Hardin, 1955; Benseler, 1968). On a per seed basis, the above estimates would be increased three to six times. Even on a per ovule basis, pollen production by *A. californica* appears to be higher than other entomophilous and even some anemophilous woody plants (Pohl, 1937).

In order to test the possibility of some degree of wind pollination in California buckeye, pollen traps were placed in trees at local populations following the technique of Hoekstra (1965). Only nine buckeye pollen grains were found distributed among seven of the 140 pollen traps set out. The grains are sculptured and sticky and the stigma is hardly suitable for collecting airborne pollen. Externally, the stigma appears to be no more than the pointed end of the style. Microscopic examination of longsections through the tapered style revealed the stigmatic surface to be a chamber at the apex. This apical chamber divides into three canals, each of which courses through a carpel. With wind as the vector, success in this difficult pollen placement would be highly unlikely.

Insect Visitors. The abundance and variety of insects actively visiting California buckeye flowers were assessed at all the study areas. Representatives of over 40 genera and 19 families were collected, of which 56 percent of the species were Lepidoptera and 17 percent Hymenoptera (Table 2). The remaining 27 percent, distributed among Coleoptera, Diptera, Hemiptera, and Neuroptera, were innocuous insects incapable of pollination.

Honeybees (*Apis mellifera*) were active and abundant at all study areas. Honeybees have been reported as common pollen and nectar gatherers in *Aesculus* in Europe (Knuth, 1908; Kugler, 1336; Sussenguth, 1936). Close observation of their activities in *A. californica* inflorescences led to the conclusion that their effectiveness as pollinators is very poor. Because of their small size, they pass under and rarely come in

TABLE 2. INSECT VISITORS (HYMENOPTERA AND LEPIDOPTERA) COLLECTED FROM CALIFORNIA BUCKEYE. *** = collected at all study populations; ** = collected at $\frac{1}{2}$ or more of the study populations; and * = collected at $\frac{1}{4}$ to $\frac{1}{2}$ of the study populations.

HYMENOPTERA

- Honeybee, *Apis mellifera* L.***
 Bumblebees, *Bombus bifarius* Cress., *B. vosnesenskii* Rad.
 Miningbees, *Andrena* sp., *Halictus* sp.
 Wasps, *Sphedidae*, *Vespidae**

LEPIDOPTERA

- Common Checkerspot, *Euphydryas chalcedona* (Dblly.)**
 California Sister, *Limnitis (Adelpha) bredowi californica* (Butler)
 Callippe Fritillary, *Speyeria callippe* (Bdv.)
 Mylitta Crescent, *Phyciodes mylitta* (Edw.)
 Rustic Anglewing, *Polygonia faunus rusticus* (Edw.)
 Mourning Cloak, *Nymphalis antiopa* (L.)
 Buckeye, *Junonia coenia* (Hbn.)
 California Ringlet, *Coenonympha californica* West. & Hew.*
 Satyrs, *Cercyonis pegala ariane* Bdv.
 Hairstreaks: *Strymon adenostomatis* (Hy. Edw.), *S. saepium*, (Bdv.)*,
S. auretteorum (Bdv.), *S. californicum* (Edw.), *S. melinus* (Hy. Edw.)
 Gorgon Copper, *Lycaena gorgon* (Bdv.)
 Acmon Blue, *Plebejus acmon* (West. & Hew.)
 Skippers, *Hesperia lindseyi* (Holl.), *Ochlodes agricola* (Bdv.)
 Common Sulphur, *Colias eurytheme* Bdv.
 Swallowtails, *Battus philenor* (L.), *Papilio eurymedon* Lucas, *P. rutulus* Lucas
 Moths, *Agrotis ypsilon* Rott., *Peridroma margaritosa* (Haw.), *Eupithecia* sp.
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contact with the anthers or stigmas as they crawl over the flowers collecting nectar. Even when foraging for pollen, they do not come near the stylar tip. Furthermore, pollen and/or nectar are toxic to worker bees as well as to larvae in the hives (Vansell and Todd, 1932; Eckert, 1933). Honeybees were frequently observed wandering aimlessly, as if in a stupor, over the inflorescences and eventually falling off and dying. It is important to note that the honeybee was first introduced into California in 1852 (Watkins, 1966); native insects do not seem adversely affected by the pollen or nectar. Thus we may rationalize the apparent contradiction of a plant poisoning an active pollinator.

Next to honeybees, the most frequent visitors were butterflies, the most common being the checker spot, *Euphydryas chalcedona*. Butterflies and a few moths observed at night appeared to be effective pollinators. They gathered nectar by traversing the length of the inflorescence, and in doing so, their flapping wings brushed against the anthers and the styles and thus could effect transfer of pollen grains into the stigmatic canal. *Aesculus parviflora*, which also has long stamens and styles, is pollinated by moths and butterflies (Knuth, 1908; de Wet, 1967) and perhaps even birds (Jaeger, 1961).

Despite the high pollen grain to seed ratio and the possibility of adequate pollen transfer by Lepidoptera, pollination still may be ineffectual.

Sampling of individual trees revealed that only about 10 percent of the gynoecia of bisexual flowers formed mature capsules. In many trees, gynoecial abortion exceeded 90 percent. Those trees that formed only a few bisexual flowers generally failed to form any fruit at all.

Compatibility. Patterns of insect activity observed suggested that most pollinations in California buckeye involve the transfer of pollen from flower to flower within a given tree (geitonogamy). Are these pollinations successful, resulting in fertilization and potential seed formation, or is outcrossing necessary? Moreover, is there any evidence of apomixis?

On nine trees at the local study areas, 352 flowers were individually tagged and were self- and cross-pollinated by hand or not pollinated. All of the latter (72) and 145 (73 self-pollinated and 72 cross-pollinated) of the others were isolated with Kraft paper bags. Of the 135 unbagged flowers, 68 were self-pollinated and 67 were cross-pollinated. The flowers tested were emasculated and all other flowers and buds in the inflorescences were removed. Fresh pollen for cross-pollinations was collected at least 1 km from the study trees and was carefully applied with a brush to the stigmatic surfaces. The paper bags, 30 cm long, were placed over the entire rachis and taped securely around the peduncle. The bags were left in place for two weeks following pollinations. Ovary enlargement and fruit development were checked weekly.

No unpollinated flowers set seed, so apomixis is unlikely. Often, gynoecia dried up and the flowers dropped off before or soon after the bags were removed. Of the bagged, pollinated flowers, only seven formed single-seeded capsules; four of these were self-pollinated and three cross-pollinated. The unbagged, pollinated flowers formed only nine single-seeded capsules, of which six were from selfing and three from crossing. The few successful hand pollinations were not restricted to any one tree or locality; moreover the low numbers of isolated flowers to mature fruits cannot be attributed to unfavorable conditions in the paper bags. Self- and cross-pollinations were equally effective or ineffective. The trees used in the compatibility experiments produced average fruit crops, i.e., 5 to 10 percent of the bisexual flowers set seed; therefore, attempts to exceed natural seed set by means of hand pollinations were unsuccessful.

CONCLUSIONS

Aesculus californica is andromonoecious and despite high bud and floral mortality of both floral types, the ratio of staminate to bisexual flowers is extremely high. Heithaus et al. (1974) have suggested that such a condition may be a specialization for pollination by pollen vectors that have a large surface area as compared to stigma size. Production of large amounts of pollen, therefore, may be associated with buckeye's dependence upon large pollen vectors such as lepidopterids for successful deposition of small pollen grains into a small stigmatic chamber. Nevertheless,

although lepidopterids appear to be effective pollinators, seed set is low and there is no increase in seed set when stigmas are self- and cross-pollinated by hand. This low seed set suggests the disruption of gametophyte development, fertilization, or early embryogeny. Several million pollen grains are produced for every mature seed, an extremely wasteful condition for an entomophilous species.

Parallels are to be seen between *Aesculus* and certain species of *Eucalyptus* that also have terminal inflorescences with many flowers, bisexual flowers with pointed styles, and relatively large fruits and seeds (Carr et al., 1971). Both taxa exhibit a definite trend towards polygamy with sterilization of bisexual flowers and increased production of staminate flowers. The adaptive and evolutionary significance of such modifications is not clear. It might be allied to the pollination system described above and also to the problem of allocating resources and supporting the growth and development of large propagules. If every flower were bisexual and matured fruit, the plant might well self-destruct under the burden.

California buckeye can tolerate such anomolous floral conditions, breeding system, and low seed output because it is long-lived and a vigorous sprouter. The "survival of the fittest" does not necessarily imply that only the perfect persist, but rather survival is granted to those equipped to make it by whatever means available. Buckeye's sexual strategy may be inefficient from an evolutionary standpoint; nevertheless, its reproductive methods suffice under existing environmental conditions.

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RELATIONSHIPS OF TRACYINA AND RIGIOPAPPUS (COMPOSITAE)

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The relationships between *Tracyina* Blake and *Rigiopappus* Gray have been discussed briefly by various authors (e.g., Blake, 1937; Raven and Kyhos, 1961) but not until recently have the morphological characters of these monotypic genera been discussed in any detail. Van Horn (1973) and Robinson and Brettell (1973) suggest that despite their traditional placement in different tribes, these two genera are similar to each other in a number of respects, also resemble *Chaetopappa* and *Pentachaeta* (both Astereae), and properly belong in Astereae. In this paper we present additional evidence, from chromosomal, biochemical, and hybridization studies, that indicates unequivocally that *Tracyina* and *Rigiopappus* are very closely related to each other.

METHODS AND MATERIALS

In 1960 the first author collected achenes of *Tracyina rostrata* Blake from the type locality (Alder Point, Humboldt County, California, *Ornduff 6185*, UC), one of two sites at which this rare species is known to occur (Keck, 1959). Plants of this annual species have been grown at the University of California Botanical Garden on several occasions since the initial collection; these cultivated plants were used in this study. *Rigiopappus leptocladus* Gray is widespread in the western United States, and three collections of this species were used in this study (Mount Hamilton, Santa Clara County, California, *Ornduff 6045*; Lake Berryessa, Lake County, California, *Ornduff 6108*; Scott Mountain, Trinity County, California, *Ornduff 6273*, all UC).